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Soil profile alteration and humus accumulation during heathland-forest succession in NW Germany

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Summary

Comparative morphological and chemical analyses were carried out in mineral and organic soil profiles under three different vegetation types in the Lüneburger Heide, NW Germany. Two stands each of *Calluna vulgaris* heathland, birch-pine forest, and oak-beech forest were selected on comparable parent material (base-poor sandy deposits of the penultimate Ice Age) in close proximity to each other. The three vegetation types are assumed to represent early, mid and late stages of a secondary succession on heathland. Orthic podzol was the dominant soil type under heathland and also under recent birch-pine forest which established naturally on former heathland. Under old-growth oak-beech forest, spodo-dystric cambisols dominated. Thirty-nine to 85 years of mixed pine-birch forest growth on former orthic podzols under *Calluna* apparently did not markedly alter the morphology of the mineral soil profile except for a tendency to less sharp horizon boundaries in the upper profile. Analysis of at least eight profiles per ecosystem type revealed more pronounced differences in the morphological and chemical properties of the organic profiles than in the mineral soil profiles under the three vegetation types. Total carbon in the mineral soil profile decreased from the heathland to the birch-pine forest and the oak-beech forest while total nitrogen stocks were rather similar. Soil acidity was similar under the three vegetation types and was not correlated with the recently visible degree of podzolization. Carbon and nitrogen pools in the organic profile increased from the heathland to the birch-pine forest and to the oak-beech forest 2.8 and 4.7fold (C) and 2.0 and 4.0fold (N) with an increasing depth of the organic layer. However, only minor differences were found in the morphological properties and C/P ratios of the organic layer under the three vegetation types. All were classified with the Moder order. C/N, C/K and C/Mg ratios (but not C/P and C/Ca ratios) were somewhat higher for the organic layer of the birch-pine forest than for heathland and oak-beech forest.

Calluna heathland, depodzolization, *Fagus-Quercus* forest, humus accumulation, humus profile, NW Germany, pioneer forest, podzol morphology, secondary succession.

Introduction

The effects of vegetation on soils have attracted the interest of pedologists, ecologists, and foresters for a long time. Much attention has been paid to the fact that, in the sandy diluvial lowlands of N Germany, well developed orthic podzol profiles are more or less restricted to anthropo-zoogenic heathlands and man-made coniferous forests. Under the autochthonous broad-leaved *Fagus* and *Quercus* forests, however, only slightly podzolised soil types such as dystric and spodo-dystric cambisols are dominant on similar geological parent material (Tüxen 1957; Horst 1964; Mückenhausen 1971; Ulrich 1980). Podzols found under recent oak and beech stands are commonly seen as a consequence of ericaceous vegetation occurring formerly at the site (e.g. Kundler 1956, 1963; Lüders 1964).

This situation seems to be different from the situation in England, Ireland, the Netherlands, France and Denmark where marked podzolization leading to iron or iron-humus podzols also seems to be a result of the growth of beech and oak on base-deficient sands (Turner & Watt 1939; Dimbleby 1952; Dimbleby & Gill 1955;

Havinga 1963; Mackney 1970; Guillet 1975; Andersen 1979).

While it is well established that converting broad-leaved forests into ericaceous vegetation (and also into coniferous forests) may enhance the development of podzolic characteristics in Central as well as Western Europe (Tüxen 1957; Horst 1964; Conry 1970; Buurman 1984; for conflicting observations see, for example, Havinga 1963), the pedogenetic effects of a replacement of heath by forests is still disputed. Some authors reported significant changes in soil morphology and chemistry after reforestation of heathlands (a process that was called 'depodzolization' by Dimbleby 1952; Miles & Young 1980, and Miles 1985) while others found no relevant alterations or questioned them on theoretical grounds (Stone 1975; Satchell 1980).

In the 18th century, about 60% of the landscape of the Lüneburger Heide in eastern Lower Saxony (Germany) was covered by anthropo-zoogenic *Calluna vulgaris* heathlands with less than 10% of the area left to the autochthonous broad-leaved (*Fagus-Quercus*) forests. Since that time, vast areas have either been replanted mainly with Scots pine (*Pinus sylvestris*), or have undergone a natural succession towards a pine-dominated forest community (Kremser 1980; Leuschner 1994). Today, *Calluna* heathland, pine and birch-pine forests on former heathland, and old-growth broad-leaved forests occur on similar parent material in close proximity to each other. The purpose of this study was to compare soil morphological and chemical properties that have developed under these three contrasting vegetation types on poor glacial deposits in NW Germany. Since *Calluna* heathland, birch-pine forest and oak-beech forest form a successional series, differences in the organic and mineral soil profiles will be discussed in a successional context.

Materials and methods

Study sites

The study was carried out in the area around Unterlüß in the southeastern part of the Lüneburger Heide (Lower Saxony, Germany, 52°45'N, 10°30'E). The region is part of the diluvial lowlands of Lower Saxony that consists mainly of sandy, nutrient poor sediments of the penultimate (Saale) Ice Age (Drenthe-2 stadial). In this area, *Calluna* heathlands have been created at least since the late Bronze Age (approx. 1700–1400 B.C.) by the activity of man (Overbeck 1975). The major destruction of the original Fagus and *Fagus-Quercus* forests, however, occurred in the period between approx. 1000 and 1800 A.D. The heathlands were used for sheep farming and bee keeping. Sod cutting and litter raping in the heath and also in most of the remaining forests probably have accelerated podzolising processes in the underlying soils (Ulrich 1980).

Three ecosystem types were selected for study that were assumed to represent different stages of a secondary succession from heathland to broad-leaved forest: (1) Extensively grazed *Calluna vulgaris*-heathland (*Genisto-Callunetum cladonietosum*), (2) birch-pine forest on former heathland (*Betula pendula* Roth and *Pinus sylvestris* L., *Leucobryo-Pinetum*), and (3) old-growth oak-beech forest (*Quercus petraea* (Matt.) Liebl. and *Fagus sylvatica* L., *Deschampsio-Fagetum*). The latter is supposed to represent the autochthonous forest vegetation on these substrates and it is unclear whether these sites were ever converted into heathland in earlier times.

Two examples of each vegetation type on comparable parent material were chosen for study:

CH1: *Calluna* heathland on orthic podzol with a thin organic layer; younger *Calluna* plants dominate. Grazing stopped two years ago. Rahberg (7 km E of Munster).

CH2: *Calluna* heathland on orthic podzol with a rather thick organic layer; older *Calluna* plants dominate. Grazing stopped ten years ago. Schillohsberg (4 km W of Unterlüß).

BP3: Naturally established birch-pine forest on former *Calluna* heathland on orthic podzol; max. age 30 years, up to 12 m high, 25% birch, 75% pine. A first generation of similar pioneering forest established approx. 1906 and was removed in 1966 (i. e. forest growth on former heathland for 85 years). Ground cover mostly of *Avenella flexuosa*. Rahberg (7 km E of Munster).

BP4: Naturally established birch pine forest on former *Calluna* heathland on orthic podzol; max. age 39 years, up to 16 m high, 10% birch, 90% pine. First forest generation on heathland (i.e forest growth on former heathland for 39 years). Ground cover of *Vaccinium* ssp., *Calluna vulgaris* and mosses. Schillohsberg (4 km W of Unterlüß).

OB5: Mature oak-beech forest on spodo-dystric cambisol; max. age 140 (beech) to 220 (oak) years, up to 27 m high, 10% *Quercus petraea*, 90% *Fagus sylvatica*. No ground cover. Süll (2 km W of Unterlüß).

OB6: Mature oak-beech forest on spodo-dystric cambisol; max. age 170 years, up to 34 m high, 45%

Quercus petraea, 55% *Fagus sylvatica*. Very sparse ground cover of *Avenella flexuosa*. Lüßberg (2 km E of Unterlüß).

The historical land use at the sites of study is documented by maps from 1775 and 1899 (Leuschner & Immenroth 1994).

The lower part of all soil profiles consists of stratified fluvio-glacial melt water sands (locally also sandy basal moraine material) of the penultimate (Saale) Ice Age; cover sand of periglacial origin forms the upper 20 to 60 cm of the profiles. Most profiles are covered atop with a several centimeters deep layer of more recent eolian sand. Medium-grained sand is the dominant size fraction of the sediments (40 to 60%) while the clay content is low (1 to 5%). Cation exchange capacity and base saturation are very low in all profiles (cf. Rode et al. 1993). All sites are on level terrain at about 90–100 m above sea level. The ground water table is found far below the rooting zone. Maximum distance between the six sites is approx. 18 km. The climate is of a humid suboceanic type (annual mean air temperature: 8.0° C, annual precipitation 730 mm).

For comparison, data of Rastin and Ulrich (1988) and Gönnert (1989) from birch-oak woods on former heathland and oak-beech stands, both in the central and northern Lüneburger Heide, are included in the section on soil morphological properties.

Methods of soil investigation

Soil morphological properties

For each vegetation type, at least 8 (for some analyses up to 61) profiles were investigated that were excavated within rectangular grids on the six sites. For the macromorphological description and classification of the humus profile, the definitions in Arbeitskreis Standortskartierung (1980) and Klinka et al. (1981) were used (cf. Tab. 1). The symbols O_L, O_F, and O_H stand for L, for Fa and Faq, and for H horizons, respectively.

Morphological horizons of the mineral soil profile were identified according to Kubiena (1953) and Scheffer & Schachtschabel (1989). For defining soil units in the field, the following rough scheme was applied (Tab. 2):

Analytical methods

Samples were taken in 6 to 7 horizons of the mineral soil and in 3 to 5 horizons of the organic profiles in the soil pits. Each soil sample itself consisted of several sub-samples collected in the four walls of that pit. These were mixed in order to form an average sample of a pit. In the laboratory, the samples were sieved with a 2-mm riddle and dried at 40° C for one week. pH-values were measured in deionized water (1:1) and 1 N KCl-solution. Total carbon and total nitrogen were determined with a C/N autoanalyser, total contents of calcium, potassium and magnesium in the organic samples after HNO_3 wet digestion by atomic

Tab. 1: Definition of humus forms as used in this study (following Arbeitskreis Standortskartierung 1980 and Klinka et al. 1981).

Horizons	L, Fa, (H), (Ae)	L, Faq, H, (Ahe)	L, Fa, H, (Ahe)		(L), (Fa), H, Aeh
AK STAND ORTSKART.	Xero-Moder	rohhumusart. Moder	feinhu.-reicher Moder (Fa>2 cm) (H>1.5)	feinhu.-armer Moder (Fa<2 cm) (H<1.5 cm)	mullartiger Moder
KLINKA	Xero-Moder	Mor-Moder	Lepto-Moder		Mull-Moder

Tab. 2: Approximate correlation of soil units as used in this study (according to Avery 1973; FAO-UNESCO 1974; Scheffer & Schachtschabel 1989).

Horizons	A_h, B_v, C	A_{he}, B_v, C / A_{eh}, B_h/B_v, C	A_e, B_{hs}, B_v, C / A_e, B_{sv}, C	A_e, B_h, B_s, C
Avery	Brown earth	Brown podzolic soils		Podzol
FAO-UNESCO	Dystric Cambisol	Spodo-dystric Cambisol	Cambic Podzol	Orthic Podzol
Scheffer & Schachtschabel	Saure Braunerde	Podsolige Braunerde	Br.erde-Podsol/ Podsol-Braunerde	(Eisen-Humus-) Podsol

absorption spectrometry. Total phosphorus was determined in the organic horizons photometrically after HNO_3 digestion. Humic and fulvic acids of the soil organic matter were fractionated mainly following Stevenson (1982): soluble humic substances were extracted with 0.5 N NaOH, humic acids and fulvic acids were separated using 1 N H_2SO_4. This was done for samples from 4 to 5 horizons of each 3 profiles per vegetation type.

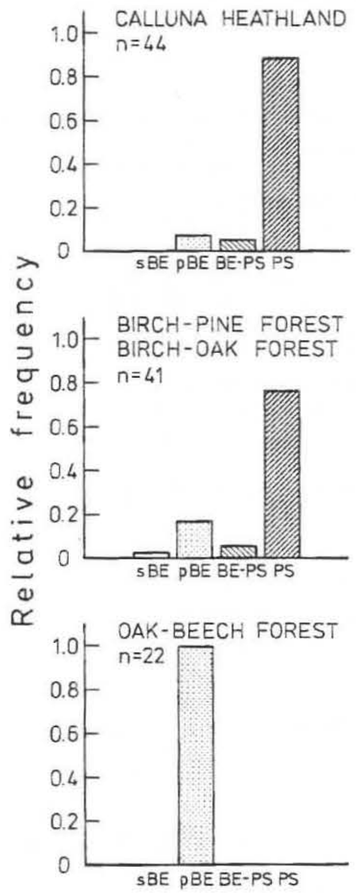

Fig. 1: Relative frequency of morphologically determined soil profile types found under various stands of three different vegetation types in the central Lüneburger Heide.

sBE (saure Braunerde), pBE (podsolige Braunerde), BE-PS (Braunerde-Podsol/Podsol-Braunerde), PS (Eisen-Humus-Podsol), compare Tab. 2.

Results

Morphological signs of podzolization

As expected mineral soil profiles with pronounced morphological signs of podzolization such as distinct eluvial and illuvial horizons were much more common under *Calluna* heathland than under oak-beech forest (Fig. 1: top and bottom). Under the latter stands with an assumed permanent forest cover, all profiles were classified as spodo-dystric cambisols while none was recognised as orthic podzol. Growth of mixed birch, pine and oak forest on former heathland podzols in most cases did not lead to marked morphological changes in the mineral soil profile after 40 to 85 years following its natural establishment: orthic podzols were still the dominant soil type under these forests in more than 40 investigated profiles (Fig. 1: centre).

Differences in morphology were chiefly detected in the nature of the organic horizons (see below) and, less visibly, in the colour of, and the boundaries between, the mineral soil horizons. As compared to podzols under *Calluna*, most orthic podzols under pine and birch had less pronounced (i.e. only weakly bleached) eluvial (A_{he}/A_e) horizons, more gradual boundaries between the illuvial (B_h, B_{sh}) horizons and a root-containing brownish B_{vsh}-horizon in the lower part of the profile. Horizon differentiation in the top-soil in an uppermost dark (humus-rich) and an underlying whitish (bleached) A horizon (A_{eh}/A_{he} and A_e) was less pronounced under the birch-pine forest than under the heathland.

Although all organic profiles that were investigated under the three vegetation types belonged to the Moder class, dominant moder types under *Calluna* heathland, birch-pine and oak-beech forest were different (Fig. 2). In the heathlands, by far the most widespread type was a summer-dry, thin (2 to 3 cm deep) Xero-Moder that also occurred with a frequency of 25% in the birch-pine forests. In the birch-pine forests, most profiles had much deeper and less xeric OF horizons and, consequently, Mor- and Lepto-Moders prevailed (rohhumusartiger and feinhumusreicher Moder). These organic profiles contrasted sharply with the thin Xero-Moders in the heathlands from which they must have originated. The most frequent humus form in both the birch-pine and the oak-beech forests was Mor-Moder.

Humus forms that are commonly associated with a more rapid litter decomposition such as Mull-Moder only occurred locally in the oak-beech forests (Fig. 2: bottom) while xeric Moder forms were completely absent here.

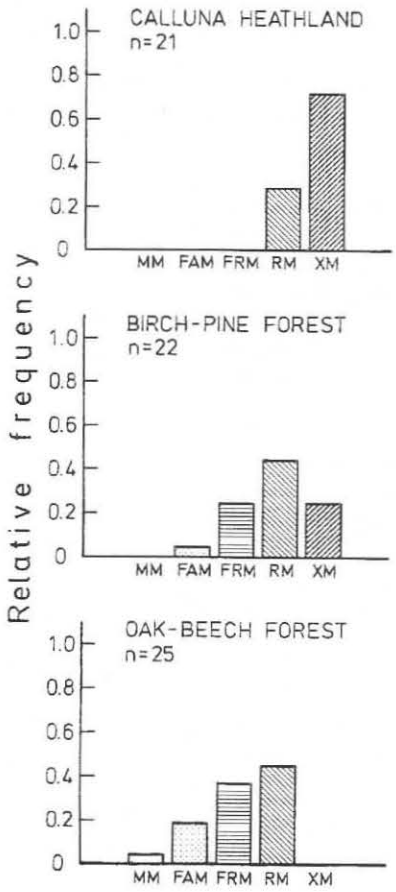

Fig. 2: Relative frequency of morphologically determined organic profile types found under three different vegetation types in the area of Unterlüß (central Lüneburger Heide).

MM (mullartiger Moder), FAM (feinhumusartiger Moder), FRM (feinhumusreicher Moder), RM (rohhumusartiger Moder), XM (Xero-Moder), compare Tab. 1.

Soil acidity, degree of podzolization and recent vegetation

In all mineral soil profiles, low pH(KCl) values between 2.5 and 4.5 were found. Differences between the three vegetation types were small. Similarly, the organic profiles under the four different tree species in the stands showed only small differences in their acidity: Organic layers formed by *Pinus*-needles had slightly lower pH(KCl) values in both their O_F and O_H horizons than litter of *Betula* in the same stand (Fig. 3: centre). On the other hand, the organic layer under *Fagus* and *Quercus* in the oak-beech forest showed pH values that were similar to each other and also to organic profiles under *Betula* in the birch-pine forest (Fig. 3: bottom).

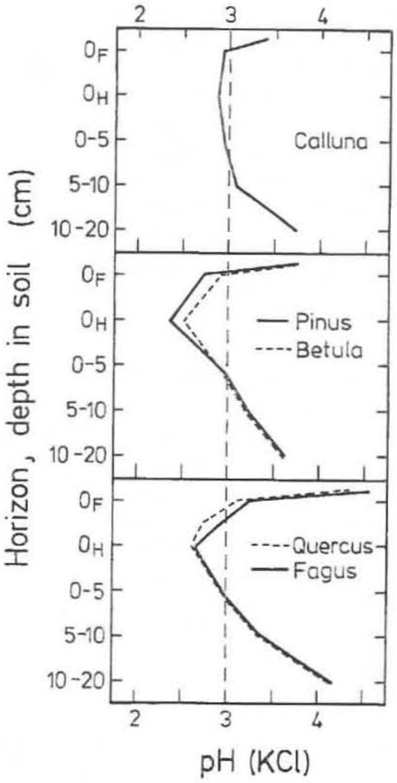

Fig. 3: Vertical change of pH(KCl) values in the organic profile and mineral topsoil under *Calluna* heathland, *Pinus* and *Betula* trees in the birch-pine forest, and *Quercus* and *Fagus* trees in the oak-beech forest in the Unterlüß area.

Data refer to mean values of eight to ten profiles each.

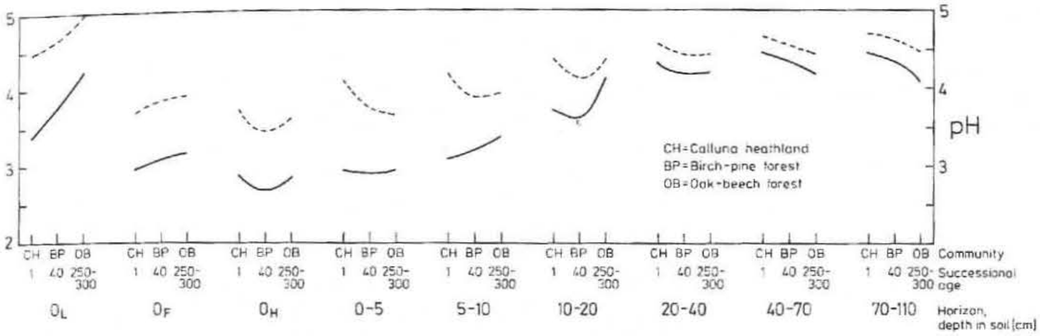

Fig. 4: pH values measured in KCl (solid line) and H_2O (dashed line) in nine horizons under *Calluna* heathland (CH), birch-pine forest (BP) and oak-beech forest (OB) in the Unterlüß area.
Data refer to mean values of eight to ten profiles each. pH(H_2O) values were taken once in October.

Minimum values of pH(KCl) regularly occurred at the bottom of the organic layer (O_H) and in the eluvial horizon (A_e) where maximum uptake of NH_4^+ is to be expected (Fig. 4). In these horizons, a considerable amount of exchangeably bound acidity exists as is indicated by the magnitude of difference between pH(KCl) and pH(H_2O)values. These pH minima were somewhat lower for the birch-pine forests (pH(KCl): 2.50 in the O_H) with a rapidly increasing humus layer than for both the oak-beech forests and the *Calluna* heathlands (pH(KCl) 2.60 and 2.88 in the O_H, respectively). In contrast, pH-values increased from the *Calluna* heathlands to the birch-pine forests, and further to the oak-beech forests in the upper (fresh) layers of the organic profile (Fig. 4).

At 10–20 cm, the spodo-dystric cambisols under oak-beech forest showed markedly lower proton concentrations than orthic podzol profiles under both *Calluna* heathland and birch-pine forest (Fig. 4). This coincides with well defined carbon and aluminium/iron accumulation (B_h and B_s) horizons at this depth in the orthic podzols. These horizons were less marked in the spodo-dystric cambisols under oak-beech forest (see above).

Carbon and nitrogen contents

The vertical change of carbon and nitrogen concentrations in the mineral soil profile revealed influences of both the soil type and the vegetation type. Distinct maxima of C and N in illuvial and minima in eluvial horizons as are typical for podzols did not occur in the spodo-dystric cambisols under oak-beech forests (Fig. 5). Consequently, the upper mineral soil of these profiles contained less carbon and nitrogen than the orthic podzols. When comparing orthic podzols under birch-pine forests and *Calluna* podzols, in the latter profiles, carbon and nitrogen concentrations were generally higher in the eluvial minima and – in some cases – also in the illuvial peaks than in similar horizons of the profiles under birch-pine forest. Thus, C and N seem to be more equally distributed over the podzol profiles of the birch-pine forests; this, however, did not affect the total stocks of these elements in the mineral soil profile (see below).

The fractionation and C/N analysis of the organic matter of the upper mineral soil horizons revealed some differences with respect to type and chemical composition of the dominant humic substances present in the different soil types: The humic acid/fulvic acid quotient (HA/FA) was significantly higher at least in the Ahe and the illuvial B_{hs}-horizons of the orthic podzols than at comparable depth in the spodo-dystric cambisols (Fig. 5: right). Although the C/N quotient of the HA fraction was found to be highly variable in the samples analysed humic acids of the uppermost horizons of the *Calluna* heathlands seem to contain less nitrogen than equivalent material in the oak-beech forests (Fig. 5: right). Differences in the nature of the soil organic matter of the orthic podzols and the spodo-dystric cambisols are also reflected by markedly higher C/N ratios of the total organic matter in the uppermost podzol horizon indicating an accumulation of nitrogen poor substances in this soil type (Fig. 6).

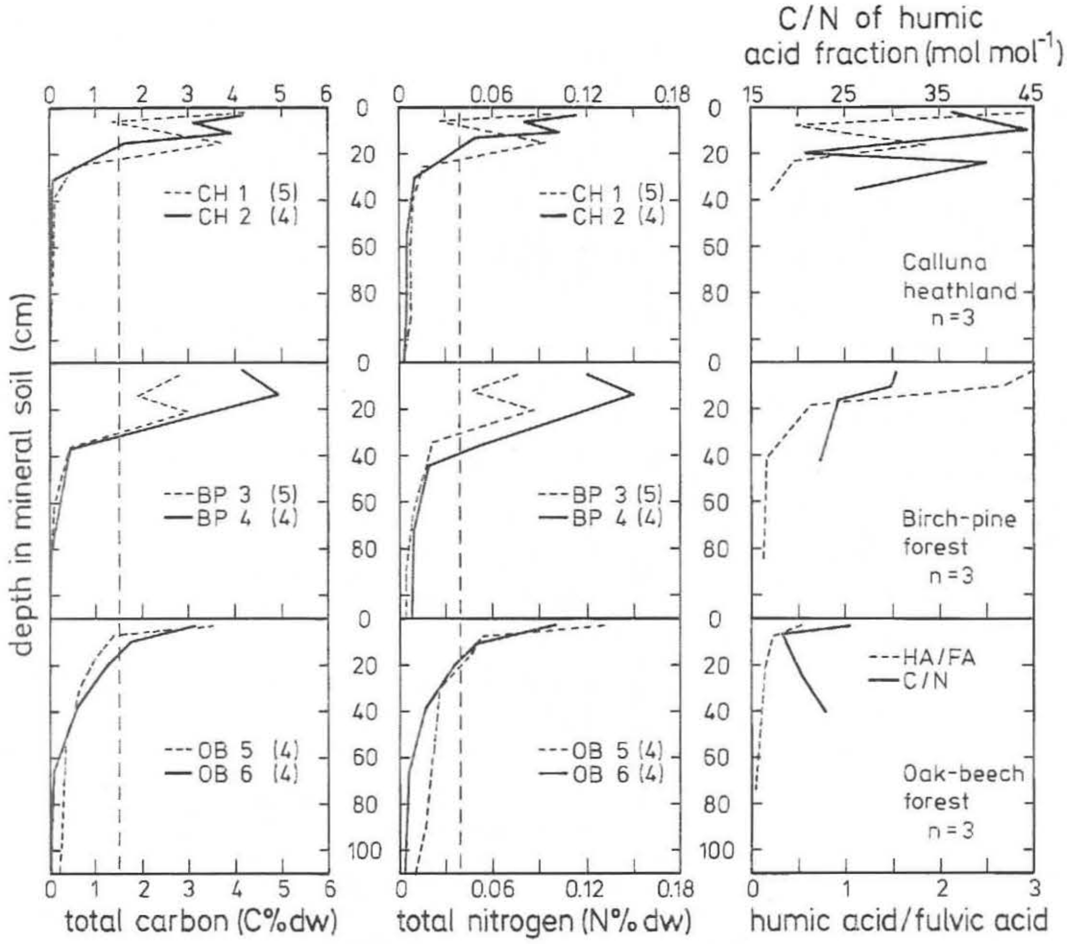

Fig. 5: (left and centre) Concentration of carbon and nitrogen in the total dead organic matter of mineral soil profiles under *Calluna* heathland (first row), birch-pine forest (second row) and oak-beech forest (third row) in the Unterlüß area.

Data refer to mean values of 4 or 5 profiles each for the heathland sites CH1 and 2, the birch-pine forest sites BP3 and 4, and the oak-beech forest sites OB5 and 6.

(right) C/N ratio of the humic acid fraction of the soil organic matter (solid line) and humic acid/fulvic acid ratio in the total dead organic matter fraction (HA/FA, dashed line) in mineral soil profiles under *Calluna* heathland, birch-pine forest and oak-beech forest (three profiles each were investigated).

In the organic profile, higher C/N ratios of the total organic substance occurred in the birch-pine forests than in the oak-beech forests (Fig. 6). Interestingly, these values were also higher than those of the *Calluna* heathlands. When comparing the organic layer under individual species in the two mixed forest stands, however, no significant differences in C/N ratios could be detected betwen competing tree species. This was true for *Fagus*/*Quercus* and also for *Pinus*/*Betula* (Fig. 6).

Carbon/(total) phosphorus ratios were found to be similar in the organic layers of all three vegetation types (Tab. 3). C/K and C/Mg-ratios of the birch-pine forest organic layer were somewhat larger than those of both other vegetation types (Tab. 3). The C/Ca-ratio declined from the heathland to birch-pine forest and to the oak-beech forest in the OF layer but not in the OH layer.

Comparing the three vegetation types reveals that the carbon content in the total mineral soil profile (0–110 cm depth) is highest in the orthic podzols under heathland, and 15 and 35% lower in the podzols under birch-pine forest and the cambisols under oak-beech forest, respectively (Fig. 7: dashed bold line). This is mainly caused by the high C concentrations in the upper 20 cm of the orthic podzols (cf. Fig. 5: left).

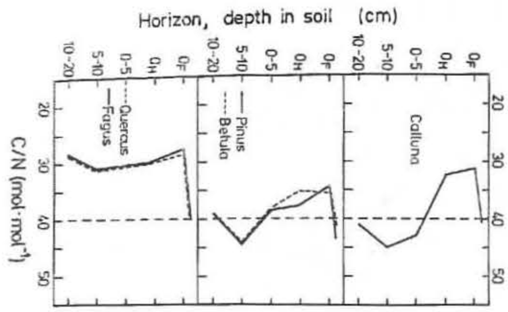

Fig. 6: C/N ratio of the total dead organic matter in organic and mineral soil profiles under *Calluna* heathland (first row), *Betula* and *Pinus* (birch-pine forest, second row) and *Quercus* and *Fagus* (oak-beech forest, third row) in the area of Unterlüß.

Data refer to mean values of eight to ten profiles each.

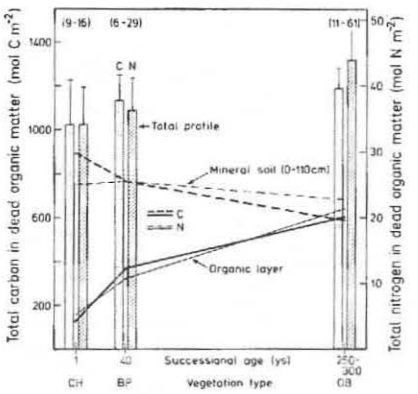

Fig. 7: Stocks of total carbon (bold lines) and total nitrogen (thin lines) in the organic layers (solid lines) and the mineral soils profiles (dashed lines) under *Calluna* heathlands (CH), birch-pine forests (BP) and oak-beech forests (OB) in the area of Unterlüß.

Data refer to mean values of 6 to 61 profiles investigated at the sites CH1 and 2, BP3 and 4, and OB5 and 6. Bars represent the totals of the organic profile and the mineral soil profile (here, mean values and standard deviation are indicated).

An opposite trend was found for the organic profiles of the three vegetation types: The carbon pool in above-ground litter increased 2.8fold and 4.7fold between the heathland and the birch-pine forest, and the heathland and the oak-beech forest, respectively (Fig. 7: continuous bold line).

Tab. 3: C/P, C/K, C/Ca and C/Mg ratios in two horizons of the organic layer of the heathland and under *Betula* and *Pinus* (birch-pine forest) and *Quercus* and *Fagus* (oak-beech forest) (in mol mol^{-1}).

Due to mineral admixtures in the organic fraction its metal content is probably somewhat overestimated in these numbers and, therefore, higher carbon/metal ratios are to be expected in the mineral-free organic substance (cf. Emmer & Sevink 1993).

	O_F horizon				O_H horizon			
	C/P	C/K	C/Ca	C/Mg	C/P	C/K	C/Ca	C/Mg
	HEATHLAND							
Calluna	1629	827	1029	1965	1703	827	1029	1965
	BIRCH-PINE FOREST							
Pinus	1621	1459	810	2084	1927	1652	889	2168
Betula	1672	1756	817	2508	1651	1258	1258	2201
	OAK-BEECH FOREST							
Quercus	1633	1304	474	2179	1776	1067	982	1218
Fagus	1498	1132	530	1941	1597	752	836	1365

The decrease in the mineral soil and the increase in the organic profile together result in rather similar pools of carbon in dead organic matter when considering the total soil profiles of heathland, birch-pine forest and oak-beech forest: The latter had only 14%, the birch-pine forests 10% more carbon stored than the heathland (Fig. 7: black bars).

Total nitrogen showed a similar increase of its pool in the organic layer when comparing the three vegetation types: a 2fold increase from the heathland to the birch-pine forest, and a 4fold increase to the oak-beech forest (Fig. 7: continuous thin line). However, in contrast to carbon, the mineral soil profiles all contained rather similar stocks of total N with only slightly higher values in the oak-beech forest (Fig. 7: thin dashed line). Thus, the resulting value of N stored in the total (mineral plus organic) profile increased from the *Calluna* heathland to the birch-pine forest and to the oak-beech forest more obviously than it did for carbon (Fig. 7: bars): The latter vegetation type had 30%, the birch-pine forest 17% higher values than the heathland.

Discussion

The comparison of a considerable number of soil profiles under three structurally different vegetation types on similar parent material indicates various changes in the organic and the mineral soil profiles that mainly have to be attributed to vegetation influence. In general, changes in the organic layer were more pronounced than in the mineral soil. Furthermore, morphological properties seem to be more affected than chemical variables in both the organic and the mineral profile.

Tab. 4: Molar ratios of total carbon and nitrogen in fresh leaf litter as collected in autumn 1990 at the research sites
(mean and standard deviation of 4 samples are given; each sample consists of 7 subsamples that were mixed, cf. Rode et al. 1993).

Calluna vulgaris	49.01	(± 1.61)
Pinus sylvestris	85.82	(± 2.84)
Betula pendula	56.76	(± 1.74)
Quercus petraea	57.52	(± 2.16)
Fagus sylvatica	56.74	(± 2.74)

Chemical composition of the organic layer

Surprisingly, the organic profiles of heathland and both forest types were all classified within the Moder order which points to a rather similar chemical composition and comparable decomposition patterns despite opposing microclimates and litter supply rates. In fact, only minor differences in the C/N and C/P ratios were found for the O_F and O_H horizons of the three vegetation types, which did not support the view of an improving litter quality in the sequence heathland – coniferous (birch-pine) forest – broad-leaved (oak-beech) forest. On the contrary, C/N (but not C/P) ratios of the O_H horizon were higher in the birch-pine forests than in the neighboring *Calluna* heathland. One factor that should influence C/N ratios in the organic profile is the nitrogen content of the fresh litter: C/N ratios of leaf litter were found to be very high for pine needles, intermediate and similar for birch, oak and beech, and, surprisingly, lowest for *Calluna* leaves (see Tab. 4).

Depth of the organic layer

Morphologically, the organic profiles are chiefly distinguished by the depths of their OF and O_H horizons that increase with a growing litter supply. The transition of heathland to birch-pine forest leads to an about 3fold increase in carbon stocks in the O_F horizon after 40 to 80 years, while the stronger humified O_H layer was only slightly affected. When comparing the birch-pine and oak-beech forests, however, a considerable increase in the O_H horizon is obvious while the O_F layers contain rather similar stocks of carbon (and other elements). The rapidly growing litter layer of the birch-pine forests is far from equilibrium: Therefore, it is to be expected that the thickness of the O_H layer will increase in time. Moreover, it explains the small contribution of this horizon to the total litter layer. In contrast, the organic profiles of the heathlands and the oak-beech forests are believed to be closer to steady-state conditions.

Litter moisture conditions represent another marked difference between the three vegetation types. Hydrological investigations showed that both the average moisture content and the maximum water storage capacity of the organic layer increases from the heathland soils to the oak-beech profiles (Dageförde, Görlitz & Leuschner unpubl. data). This should favour biologically

mediated decomposition processes under the oak-beech forest and, to a lesser degree, under the more open birch-pine canopy. Furthermore, chemical data on the organic layer (Rode et al.1993) support the view that increasing nutrient stocks which accumulate in deeper organic profiles under forest stands together with a more favourable water regime result in high fine root densities in the O_F and (to a lesser degree) the O_H layers of both forest types. In contrast, *Calluna* fine roots in the heathland podzols were found to be mainly concentrated in the Ahe and the B_{sh} horizons but were nearly absent from the drought-affected thin Xero-Moders.

Thus, irrespective of the litter quality, a growing organic layer led to an increasing concentration of active fine roots within the litter horizons. One important consequence is the fact that, in the oak-beech forests and in the successional birch-pine forests, mineralization (especially ammonification) and nutrient uptake largely occur in close proximity to each other, while in the orthic podzols under heathland, they are separated from each other in both space and time to a much higher degree.

C and N content and soil acidity in the mineral soil profiles

Orthic podzols under heathland in the Lüneburger Heide contained 35% more carbon in their mineral soil than spodo-dystric cambisols under oak-beech forests. Several factors may be responsible for this difference. Since in the uppermost 15 cm of the mineral soil profile root biomass was found to be significantly higher under the heathlands than under the oak-beech forests one may expect a higher carbon input via root decomposition in orthic podzols. A higher percolation and precipitation of organic substances in orthic podzols is indicated by the low carbon concentration in the eluvial horizons of these profiles compared to the cambisols. Whether differences in the chemical composition and degradability of the soil organic material influence the total carbon content of the mineral soil is unclear. Lower C/N ratios of the humic acid fraction, which were observed under oak-beech forest (cf. Fig. 5c) could possibly lead to a shorter mean residence time of carbon in the spodo-dystric cambisols.

Differences in soil acidity under the three vegetation types are caused by the differential strength of ecosystem-internal and external acidity sources. Data of Matzner (1980) and Bredemeyer (1987) reveal higher atmospheric deposition rates of acidity for coniferous (pine) stands than for deciduous (oak) stands and heathland in the Lüneburger Heide (1.3, 1.0, and 0.6 kmol $H^{+}*ha^{-1}*a^{-1}$). Furthermore, the importance of internal acidity sources was found to differ considerably between pine and oak forest: Bredemeyer (1987) calculated that 22 and 47% of the total proton load originated from sources within the ecosystem in the coniferous and deciduous stands, respectively. Rather high humus and biomass accumulation rates in the birch-pine and oak-beech forests, respectively, are processes which both immobilise basicity and ammonium, mainly from the bottom of the organic profile, but that are marginal in the heathland profiles. On the other hand, root system inventories showed that the upper mineral soil under heathland as well as under birch-pine forest contained higher fine root densities than the oak-beech profiles. An assumed higher ammonium uptake in these horizons of the mineral soil, therefore, might well be seen as the primary cause of the deeper extension of soil acidification in these profiles (Fig. 4).

A deep reaching acidification should be a favourable precondition for the downward movement of organic matter-metal complexes, but seems not to be sufficient for its occurrence in these soils. In fact, a comparison of the vertical distribution of pH-values under the three vegetation types leads to the conclusion that there is no strong correlation between the morphologically visible degree of podzolization (cf. Fig. 1) and recent soil acidity (cf. Figs. 3 and 4). Profiles with strongest indications for podzolization, i.e. the orthic podzols under heathland with sharp horizon boundaries and a pronounced vertical transport of humic substances, were less acidic in the O_H and the Bhs-horizon than the orthic podzols under birch-pine forest with a slightly lower degree of podzolization. Similarly, pH-values in the eluvial horizons of spodo-dystric cambisols under oak-beech forest were equal (A_{he}) or even lower (O_H) than in the orthic podzols.

Does significant depodzolization occur?

Our results did not provide evidence for a significant vegetation mediated regeneration of heathland podzols on base-deficient sandy substrates in the Lüneburger Heide. Forty to eighty-five years of pine and birch forest growth on former heathland podzols did not markedly alter the morphology of the mineral soil profile. Minor differences that were noticed in the boundaries of the horizons and an equalization of the carbon distribution in the profile are comparable to the effects of oak establishment on heathland in Denmark as reported by Nielsen et al. (1987) and Nørnberg (1991). Mückenhausen (1935) observed a slight amelioration of orthic podzols in NW Germany after establishment of deciduous forest but most podzol properties were conserved. Greve (1933) described changes in the soil profile towards an 'Oxalis-type' of podzol following growth of Scots pine on *Calluna* heathlands in the Lüneburger Heide that also did not change the chemical properties of the mineral soil in a significant manner. Dimbleby (1952) and Burrichter (1954) found an increase of faunal and microbiological activity together with a deeper root penetration after birch colonisation of heathland.

Our above mentioned results contrast with data from Miles & Young (1980) from base-poor glacial drift sands in Scotland who report a marked decrease in C/N (and C/P) ratios and increases in pH and exchangeable calcium in the uppermost mineral soil after 26 to 90 years of birch colonisation on *Calluna* heathland in Scotland. The dicrepancy with our data may partly be caused by the nature of the mixed birch-pine stands investigated here: Birch contributes only 25% and 10%, respectively, to the canopy layer and thus, *Betula* and *Pinus* litter are mixed to a certain degree in the organic layer, lowering the assumed ameliorating effect of birch litter (cf. Miles 1985).

However, it has to be kept in mind that soil profiles result from the cumulative effects of varying ecological conditions over many centuries. Therefore, a correlation between the recent degree of podzolization and the vegetation type does not necessarily prove an effect of certain plant communities on the processes underlying podzolization.

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